Beyond the border: Effects of an expanding algal habitat on the fauna of neighbouring habitats

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ABSTRACT

The impacts of novel habitat-forming organisms on associated fauna have been difficult to predict, and may affect the fauna of neighbouring habitats due to changes in the spatial configuration of habitat patches of differing quality. Here, we test whether the localised expansion of a native habitat-forming macroalga, *Caulerpa filiformis*, on subtidal reefs can affect the abundance of fauna associated with a neighbouring macroalgal habitat. *C. filiformis* was a functionally distinct habitat for fauna, and the total abundance of epifauna associated with the resident alga, *Sargassum linearifolium*, was reduced at some sites when in close proximity to or surrounded by *C. filiformis*. Experimental manipulation of habitat configuration demonstrated that the low abundance of gastropods on *S. linearifolium* when surrounded by *C. filiformis* was likely explained by *C. filiformis* acting as a physical dispersal barrier for mobile fauna. Changes to the spatial configuration of novel and resident habitats can thus affect the abundance of fauna in addition to the direct replacement of habitats by species undergoing range expansions or increasing in abundance.

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1. Introduction

Changes to the spatial configuration of habitats can have profound impacts on the abundance and diversity of associated fauna. The fragmentation of habitats in particular, where habitat patches are reduced in area and increasingly separated by an uninhabitable or low quality matrix, is widely recognized as a major challenge for the conservation of biodiversity (Debinski and Holt, 2000; Driscoll et al., 2013; Fahrig, 2003). In addition to qualities of habitat patches themselves (e.g., shape, size and distance among patches), the quality of a neighbouring habitat (Prevedello and Vieira, 2010) and processes occurring on borders between habitats (e.g., increased predation along habitat edges, Ries et al., 2004) can strongly affect the abundance and distribution of animals in the landscape.

A wide range of mechanisms result in animal abundance being affected by changes to the identity of neighbouring habitats (Underwood et al., 2014). If a neighbouring habitat of lower quality becomes more widespread, then animals in a focal habitat may decrease in abundance due to a lower availability of suitable habitat on a landscape scale or decreased likelihood of detecting the habitat (e.g., associational resistance, Atsatt and O'Dowd, 1976). Alternatively, they may increase in abundance in the focal habitat on a local scale due to individuals becoming concentrated on the remaining suitable habitat (Bergvall et al., 2006). If a neighbouring habitat is of higher quality, it may act as a sink population and draw animals away from the focal habitat (e.g., Atsatt and O'Dowd's 1976 "attractant-decoy plants"), or as a source population to the focal patch if there is net export of individuals from high quality patches supporting higher densities. Even if the neighbouring matrix cannot support individuals of a given species, its identity can affect the likelihood of predation for animals dispersing between habitat patches or abiotic conditions at habitat edges (Prevedello and Vieira, 2010). Predicting the effects of changes to habitat configuration is thus dependent on whether neighbouring habitats provide functionally equivalent habitat for associated fauna and, if not, the likely dispersal of associated fauna among patches.

The loss of habitat forming organisms (plants, macroalgae, sessile marine invertebrates) due to clearing, harvesting and environmental stress has clearly altered the spatial configuration of many habitats worldwide with subsequent impacts on biodiversity of associated fauna (Thomsen et al., 2010). Impacts on fauna are also evident due to the addition of habitat forming organisms — exotic species that have spread beyond their natural range (Crooks, 2002; Gribben et al., 2013; Wright and Gribben, 2008) and the range expansions of species native to a region (Carey et al., 2012; Sorte et al., 2010). These range expansions have mostly negative effects on co-occurring habitat formers due to competition for space and resources (Thomsen et al., 2014), but can benefit associated fauna due to the provision of higher quality food or refuge (e.g., Neira et al., 2005; Wright et al., 2014) or modifications of the abiotic environments (e.g., Gribben et al., 2013; Gribben and Wright, 2006). Whilst many of these studies describe differences in associated fauna among habitat-formers, or in contrast to unvegetated areas, few studies have considered how the spatial configuration or connectivity among habitats may contribute to observed faunal changes. Incorporating this information may help resolve the often unpredictable effects of range expanding habitat-formers on biodiversity with negative, neutral or even positive effects on organisms at other trophic levels being observed (Powell et al., 2011; Thomsen et al., 2014; Vilá et al., 2011).

Macroalgal range expansions are common in the marine environment, with over 400 cases of introductions to non-native sites, and a wide range of documented impacts on other habitat forming macrophytes, and their associated communities (Maggi et al., 2014; Thomsen et al., 2014; Williams and Smith, 2007). Yet, tests of the effects on fauna of native range expanding marine macrophytes are rare (but see Arrontes, 2002). *Caulerpa filiformis* is a green alga native to south-east Australia that appears to have increased in abundance over the last century, with increased sedimentation (Glasby et al. in press; Zhang et al., 2014) and loss of co-occurring brown algae due to pollution (Coleman et al., 2008) suggested as causal factors. It is now a dominant species on many rocky reefs in the Sydney region (Glasby et al., in press; Pillmann et al., 1997; Zhang et al., 2014) and can form mono-specific patches hundreds of meters in area. It colonises new areas by the dispersal of fragments and the vegetative growth of stolons (Khou et al., 2007) and its establishment is facilitated by disturbance, colonising disturbed patches more quickly than co-occurring macroalgae (Zhang et al., 2014).

We expect that changes to the spatial configuration of algal habitats due to the addition of *C. filiformis* to rocky reefs could affect the abundance and richness of fauna on neighbouring habitats for two main reasons. Firstly, *C. filiformis* is likely to provide a functionally distinct habitat for associated fauna due to known differences between the composition of epifauna on invasive species in this genus and co-occurring macrophytes in other marine systems (e.g. *Caulerpa* spp. in the Mediterranean, Tuya et al., 2014; Vázquez-Luis et al., 2008). Species of *Caulerpa* produce an array of non-polar secondary compounds (caulerpenynes, Paul et al., 2001) that result in tissues from this species being low preference foods for most marine herbivores (Cummings and Williamson, 2008; Davis et al., 2005). Secondly, the fauna associated with macrophytes is known to be influenced by the spatial arrangement of habitat patches. Changes to the size, shape and isolation of habitat patches (Airoldi, 2003; Murphy et al., 2010; Roberts and Poore, 2006), their orientation with respect to currents (Tanner, 2003) and variation in predation pressure and water flow along habitat edges (Hovel and Wahle, 2010; Warry et al., 2009) can all affect epifaunal abundance.

Given this potential of dense beds of *C. filiformis* to affect the fauna of neighbouring habitats, we tested whether proximity to the native range expanding macroalga, *C. filiformis* alters the abundance of epifauna inhabiting beds of the locally dominant macroalga *Sargassum linearifolium*. The specific aims of this study were to determine: (1) if *C. filiformis* represents a functionally distinct habitat for mobile epifauna, (2) whether proximity to *C. filiformis* can impact the epifaunal communities inhabiting a neighbouring macroalga, *S. linearifolium*, and (3) whether *C. filiformis* acts as a physical or biological barrier to faunal colonisation to *S. linearifolium*.

2. Material and methods

2.1. Study organisms and sites

C. filiformis (Suhr) Hering is a green macroalga found on exposed shores in New South Wales. Its range has been described as Port Stephens (32° 45′ S, 152° 12′ E) to Jervis Bay (35° 00′ S, 102° 50′ E) (Davis et al., 2005) although isolated populations have recently been noted as far north as Evans Head (28° 21′ S) (Glasby et al., in press). It occurs on both sandy and rocky substrates from 0 to 6 m depth. The species has upright, strap-like blades to >40 cm with a width of ~1 cm and forms dense beds with root-like rhizomes forming a mat on the substrate. *C. filiformis* can form extensive mono-specific beds on shallow, exposed rocky reefs and is a dominant macroalga on several rocky reefs in the Sydney region.

S. linearifolium (Turner) C.Agardh is an abundant brown macroalga of the shallow subtidal region of rocky reefs (Womersley, 1987) along the New South Wales coast. It forms dense beds, as well as occurring in smaller patches and as isolated individuals within other macrophyte beds. The species has a structurally complex thallus to 50 cm in height and is habitat for a diverse and abundant assemblage of mobile invertebrate groups including amphipods, isopods, copepods, gastropods and polychaetes (Poore et al., 2000; Roberts and Poore, 2006). The turf habitat adjacent to both *C. filiformis* and *S. linearifolium* comprises a complex of the articulated coralline red algae *Corallina officianalis* Linneaus and *Amphiroa anceps* (Lamarck) Decasine, filamentous algae and trapped sediments. Coralline turfs in the Sydney region are known to provide habitat for a diverse and abundant assemblage of mobile invertebrates (Kelahar, 2003).

Sampling and experiments were conducted at three locations within the Sydney (Mona Vale, 33°40′33″ S, 151°19′06″ E, and Dee Why, 33°45′16″ S, 151°17′54″ E) and Illawarra regions (Bulli Point, 34°20′19″ S, 150°55′37″ E) of New South Wales, Australia. The sites chosen each had an extensive population of *C. filiformis* as well as adjacent patches of *S. linearifolium* and coralline algal turf habitats. All sites are shallow exposed rocky reefs, with *C. filiformis* occupying the reefs from low tide level to ~3 m depth at Dee Why, from the low tide level to ~5 m depth at Mona Vale, and from just above the low tide level to ~5 m depth at Bulli.

2.2. Epifauna of C. filiformis

To confirm that *C. filiformis* is a functionally distinct habitat for epifauna, and thus would separate patches of *S. linearifolium*, we contrasted the fauna inhabiting *C. filiformis* to that inhabiting *S. linearifolium* and to the coralline turf habitat which also separates patches of *S. linearifolium*. Establishing differences between these habitats is essential for interpreting any variation in the fauna on the *S. linearifolium* habitat in relation to its proximity to *C. filiformis*.

Six samples from interspersed patches of each habitat (*C. filiformis*, coralline turf and *S. linearifolium*) were taken from Dee Why, and consisted of all of the algae, surface substrate, and associated invertebrates from within a standardized 50.6 cm^2 core. A standardized area of habitat within a core was used due to the very different physical structures of each habitat, and the difficulty